

Prospects for Importation Biological Control of the Soybean Aphid: Anticipating Potential Costs and Benefits

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ABSTRACT We discuss the potential pros and cons of using importation biological control against the soybean aphid, *Aphis glycines* Matsumura (Homoptera: Aphididae). Importation of exotic organisms for biological control is never completely risk-free, but the potential negative impacts of not achieving biological control of invasive pests may exceed the risks associated with a biological control introduction. The potential benefits of biological control include reduced insecticide use and a reduced ability of the invasive pest to impact native flora and fauna, and we outline what the scope of these benefits may be for the soybean aphid. The benefits are only accrued, however, if biological control is successful, so the likelihood of successful biological must also be assessed. Accordingly, we outline some issues relevant to predicting the success of importation biological control of the soybean aphid. We also outline the potential risks to nontarget organisms that would be associated with importation biological control of the soybean aphid. Currently, two parasitoid species, *Aphelinus albipodus* Hayat and Fatima (Hymenoptera: Aphelinidae) and *Lipolexis gracilis* Förster (Hymenoptera: Braconidae) have been imported from Asia and have passed through quarantine. We briefly review the biology and host range of these two species. A different strain of *A. albipodus* that was released against the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae), in the early 1990s was also found to attack the soybean aphid in the laboratory and has been redistributed from Wyoming to Minnesota and Wisconsin in field releases against the soybean aphid. We discuss our rationale for going forward with this redistribution.

KEY WORDS soybean aphid, biological control, *Aphelinus albipodus*

IMPORTATION BIOLOGICAL CONTROL IS being considered as an option for obtaining long-term, sustainable management of the soybean aphid, *Aphis glycines* Matsumura. However, biological control programs do not occur in an ecological vacuum and each introduction carries with it some unknown level of environmental risk (Hokkanen and Lynch 1995, Follett and Duan 2000, Wajnberg et al. 2001). These risks must be weighed against the consequences of not initiating biological control, which can also include serious environmental as well as economic and health risks. Balancing these risks to determine the best possible course of action in the face of an exotic pest invasion is not easy, but it is a necessary step in developing a rational basis for invasive species management in general, and importation biological control in particular. In a practical sense, there are two decisions to be

made: is importation biological control warranted, and if so, which species should be introduced? The answer to the first question rests on the severity of the pest problem. In our view, importation biological control should be considered if significant and consistent environmental damage, economic hardship, or human health problems are being caused by the invader. Biological control is not warranted, however, unless suitable and promising biological control agents can be identified for importation. If this is the case, deliberations concerning which species should be released come into play. Here, species should be chosen that both minimize risks to nontarget organisms and provide the best chance for successful control of the invader. These goals may sometimes be at odds with one another, and in this case, decisions concerning compromise solutions may have to be made.

In this article, we consider importation biological control of soybean aphid within this context. We outline the anticipated risks of doing and not doing biological control and then discuss the prospects for introducing effective natural enemies from the native range of the soybean aphid by focusing on species that are now in culture.

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Table 1. Threatened and endangered Fabaceae within or near the current distribution of soybean aphid

Species	Common name	Status	Distribution
<i>Aeschynomene virginica</i> L.	Sensitive joint-vetch	Threatened	PA, NJ, VA, MD, NC, SC
<i>Apios priceana</i> Robinson	Price's potato-bean	Threatened	IL, KY, TN, MS, AL
<i>Astragalus bibullatus</i> Barneby and Bridges	Pyne's (=Guthrie's) ground-plum	Endangered	TN
<i>Dalea foliosa</i> (Gray)	Leafy prairie-clover	Endangered	IL, TN, AL
<i>Lespedeza leptostachya</i> Engelm	Prairie bush-clover	Threatened	MN, IA, WI, IL
<i>Oxytropis campestris</i> L. var. <i>chartacea</i>	Fassett's locoweed	Threatened	WI
<i>Trifolium stoloniferum</i> (Muhl.)	Running buffalo clover	Endangered	KS, MO, AR, IL, IN, OH, KY, WV

USDA, NRCS. 2001. The PLANTS Database, Version 3.1 (<http://plants.usda.gov>). National Plant Data Center, Baton Rouge, LA.

Potential Costs and Benefits of Releasing Natural Enemies Against Soybean Aphid

Potential Benefits of Biological Control

There are two related potential benefits of releasing exotic natural enemies against the soybean aphid in North America. Both are predicated on the releases resulting in successful biological control. First, successful biological control may regulate the soybean aphid below economic thresholds and therefore reduce or eliminate the need for costly and environmentally damaging insecticide applications. In the context of soybean aphid, widespread insecticide use in the face of damaging soybean aphid populations is a virtual certainty, given field trials demonstrating the efficacy of spray programs against this pest (Ostlie 2001).

The second potential benefit of successful biological control is that it could reduce the likelihood of soybean aphid invading new agricultural and natural habitats. While the aim of biological control is not pest eradication, average pest densities can be lowered by three or more orders of magnitude in successful biological control projects (Beddington et al. 1978). Substantially lower densities in one habitat (soybean fields and *Rhamnus* stands) should decrease the size of populations invading new habitats and therefore decrease the likelihood of establishment in the new habitat (Hopper and Roush 1993, Memmott et al. 1998). Of course, if chemical control lowers soybean aphid numbers to levels at or below those achieved by successful biological control, this benefit could be achieved equally well, or more effectively, using chemical control. In this case, however, associated environmental and financial costs would be incurred.

An example of an agricultural commodity that may be at risk is snap beans, where soybean aphids have been implicated in the spread of plant-pathogenic viruses. Soybean aphids have been identified as likely vectors of a number of nonpersistently transmitted plant viruses, including alfalfa mosaic and cucumber mosaic virus in Wisconsin, Michigan, and New York (Alleman et al. 2002, Stevenson and Grau 2003, Thompson and German 2003). Also, published reports of successful transmission of tobacco vein-banding mosaic virus (a variant of potato virus Y) by the soybean aphid may put the seed potato industry at risk by

introducing another vector into this pathosystem (Fang et al. 1985). In both of these cases, pathogenic viruses can be spread by casual feeding or probing; neither snap beans nor potatoes need to be preferred by soybean aphid to receive viruses vectored by soybean aphid.

Biological control may also decrease the extent to which soybean aphids escape into natural ecosystems. In this way, biological control could decrease detrimental impacts on native plants and aphids and restrict unwanted natural enemy enhancement. Below, we outline some of the detrimental environmental impacts that soybean aphids may have if they escape into natural ecosystems.

Detrimental Impacts on Native Legumes. Secondary (summer) hosts of the soybean aphid in Asia include not only the cultivated soybean, but also wild *Glycine* species (Wang et al. 1994), some tick clovers (*Desmodium* spp.), and kudzu (*Pueraria* spp.) (Blackman and Eastop 2000, Ragsdale et al. 2004, Wu et al. 2004). High levels of reproduction of soybean aphid have also been demonstrated on red clover, *Trifolium pratense* L., and crimson clover, *T. incarnatum* L., with limited reproduction reported from berseem and kura clover (*T. alexandrinum* L. and *T. ambiguum* Bieb., respectively) (Alleman et al. 2002). While none of these clovers are native to North America, their use by the soybean aphid suggests that legumes other than soybean can be used as hosts. Indeed, winged soybean aphids have been collected from Minnesota plantings of purple prairie clover, *Dalea purpurea* Vent., a native prairie legume (Ragsdale et al. 2004). There are a number of native legume species that are either endangered or threatened and that occur within the current range of soybean aphid (Table 1). More research is needed on the potential for soybean aphid to develop on legumes native to North America. Just as an estimate of natural enemy host/prey range can be included in an assessment of the risk of biological control to nontarget organisms (see below), an estimate of the host range of soybean aphid itself can be included in an assessment of the risk of *not* controlling soybean aphids (by biological or other means).

Detrimental Impacts on Native Overwintering Hosts. The genus *Rhamnus* L. is represented by over 100 species, most being native to temperate regions of the northern hemisphere (Rehder 1940, Smith 1977).

Several species are common in the United States, but the most prevalent species have become naturalized here after being introduced from Europe or Asia. *R. cathartica* L., *R. frangula* L., and *R. davurica* Pallus were brought to the United States for use in ornamental landscaping. Others, such as *R. caroliniana* Walt. and *R. lanceolata* Pursh, are native, and their distribution overlaps with that of the soybean aphid. The range of a third North American native, *R. alnifolia* L'Hér., also overlaps with that of the soybean aphid and is considered an endangered species in Illinois (<http://dnr.state.il.us/espb/datelist.htm>). In a field-cage study in which soybean aphids were exposed to 11 putative winter hosts within the Rhamnaceae, successful overwintering of eggs was only documented from *R. cathartica* and *R. alnifolia* (Voegtlin et al. 2004). The impact of soybean aphid on the native *R. alnifolia* must therefore be a concern.

Displacement of Native Aphids Through Resource Competition. If soybean aphids were to establish within a natural ecosystem, native aphids or other herbivores could in principle be impacted through resource competition. Although interspecific competition among insect herbivores is sometimes dismissed as being relatively weak (Strong et al. 1984), there are some examples of resource competition among aphid species. Moran and Whitham (1990), in particular, documented strong suppression of the root feeding *Pemphigus betae* Doane by the gall-forming leaf feeder *Hayhurstia atriplicis* L. Gall-forming insects are often particularly proficient at diverting plant nutrients to the site of gall formation, and in the case of this system, the nutrient drain from root tissues was apparently strong enough to severely impact *P. betae*. Milder forms of competition have been documented among aphid species feeding above ground as well, however (e.g., Addicott 1978, Antolin and Addicott 1988).

Natural Enemy Enhancement. Soybean aphids invading natural systems could lead to an increase in densities of natural enemies, thus putting native herbivores or other insects at risk through "apparent competition" and other indirect effects (Holt and Lawton 1994). For instance, soybean aphid may indirectly cause an increase in another exotic insect, *Harmonia axyridis* (Pallas), a lady beetle that has recently become established in the North Central United States (Koch 2003). Increasing the abundance of this coccinellid beyond current levels could exacerbate current negative influences that include possible displacement of native coccinellids (Brown and Miller 1998, Colunga-Garcia and Gage 1998, Michaud 2002b) and predation on eggs of the Monarch butterfly (Koch et al. 2003).

Interactions Involving Ants. Soybean aphids could attract ants (native or introduced) into agricultural or natural ecosystems. In soybean fields, ants can be either detrimental or beneficial, but it is conceivable that the presence of aphid-tending ants would facilitate the emergence of other potential honeydew-producing pests of soybeans, such as whiteflies or the cotton aphid, *Aphis gossypii* Glover. In natural systems, the presence of ant/aphid mutualisms can

have pervasive effects on community structure, including strong suppression of biodiversity (Wimp and Whitham 2001).

Potential Costs of Biological Control

The potential costs of releasing biological control agents include attack of nontarget hosts in natural systems and unintended negative indirect effects stemming from the releases. The necessity to anticipate nontarget effects has been emphasized in a number of recent publications concerning actual, suspected, or hypothesized unintended side effects of biological control introductions (e.g., Howarth 1991, Simberloff and Stiling 1996, Boettner et al. 2000, Follert and Duan 2000, Pearson et al. 2000, Strong and Pemberton 2000, Henemann and Memmott 2001, Wajnberg et al. 2001, Lynch et al. 2002, Michaud 2002a, Schellhorn et al. 2002, Benson et al. 2003, Louda et al. 2003, Secord 2003). It is also widely recognized, however, that the degree of damage caused by invading insect pests or weeds to natural ecosystems or indigenous human cultures can be so great that it outweighs risks associated with the importation of rationally-chosen and effective natural enemies (e.g., Room 1990, Simberloff and Stiling 1996, Pimentel 2000, Porter 2000, Blossey et al. 2001, DeLoach et al. 2003, Kuris 2003).

The nontarget organisms that would be at the greatest risk by releases of exotic parasitoids against soybean aphid are native aphids. While we are not aware of any native aphid species that are endangered (Hopper 1995), there are clearly numerous native aphid species that are not pests, and some of these may be rare. Aside from their intrinsic value as members of natural communities, aphids can have very strong community level effects within natural ecosystems (e.g., Dickson and Whitham 1996, Wimp and Whitham 2001). The implication is that changes in abundance of native aphids caused by the introduction of soybean aphid parasitoids may have broad indirect effects within natural ecosystems. As is the case for a hypothetical invasion of soybean aphid into natural habitats, it is very difficult to predict negative impacts of this type that could end up being attributed to soybean aphid parasitoids. However, some possibilities are listed below.

Effects on Aphid Host Plants. Natural regulation of native plants by native aphids may be disrupted if a biological control release impacts native aphid abundance. We are aware of only a single instance where an aphid was suggested as a possible biological control agent, *Myzus lythri*, for control of purple loosestrife, *Lythrum salicaria* (Voegtlin 1995), and this insect has not been released. The fact that many aphids are major crop pests, however, attests to their ability to reduce plant fitness.

Effects on Hyperparasitism. Aphid hyperparasitism may increase with the introduction of one or more soybean aphid parasitoids, leading to suppression of other primary aphid parasitoids via apparent competition (van Nouhuys and Hanski 2000, Morris et al.

2001). This possibility was brought up by Strong and Pemberton (2001) in a discussion of potential unintended indirect effects of biological control. The susceptibility of primary aphid parasitoids to hyperparasitism is frequently known, at least in general terms (Müller et al. 1999, Brodeur 2000). Thus, the danger of unintended effects of biological control through hyperparasitism could in principle be minimized by choosing primary parasitoids with comparatively low susceptibility to hyperparasitoids.

Effects on "Beneficial" Aphids in Agricultural Settings. Introduced biological control agents may negatively impact nonpest aphids that serve as alternative prey or hosts for biological control agents of pest species or that produce honeydew that benefits biological control agents. For example, *Bathypsectes curculionis* (Thomson) is one of several biological control agents that partially control alfalfa weevil across much of the soybean growing area (Radcliffe and Flanders 1998). The longevity and fecundity of *B. curculionis* is enhanced by feeding on honeydew of the pea aphid, *Acyrtosiphon pisum* (Harris) (England and Evans 1997) and higher populations of this parasitoid are found in field plots with than without pea aphids (Evans and England 1996). The pea aphid is a recorded host of *A. albipodus* (a parasitoid of soybean aphid), and reduced populations of the pea aphid could limit the ability of *B. curculionis* to control alfalfa weevil. In another example, the presence of corn leaf aphid, *Rhopalosiphum maidis* (Fitch), in sorghum (where it is itself rarely a pest) can indirectly lead to suppression of greenbug [*Schizaphis graminum* (Ron-dani)], a serious pest of sorghum] through attraction of aphidophagous coccinellids early in the season (Kring and Gilstrap 1986).

Likelihood of Successful Biological Control

Analysis of importation biological control must balance the risks of doing biological control with the risks of not doing biological control (e.g., Pimentel 2000, Porter 2000, Hopper 2001, Lonsdale et al. 2001). However, the risks of not doing biological control are only reduced if biological control is successful. Thus, an estimate of the likelihood of biological control success must be seen as an important component of an overall risk analysis for biological control. In this section, we outline some of the considerations that could go into an estimate of the likelihood for successful importation biological control of the soybean aphid.

Although annual cropping systems are not considered the ideal habitat for biological control by introduction of exotic natural enemies, important successes have been achieved (Haynes et al. 1974, Hagen et al. 1976, van den Bosch et al. 1976), and these successes include aphids as target pests. For instance, successful biological control of the carrot aphid, *Cyrtorhinus fulvus* Knight, was achieved in Australia and Tasmania by importation of the parasitoid *Aphidius salicis* Haliday from California (van den Bosch et al. 1976). In alfalfa, a crop that is replanted every 3–5 yr but also mown three to four times each summer in much of its range,

successful classical biological control with parasitoids has been achieved against three aphid species (Clausen 1978, Gonzalez et al. 1995). Examples of aphids in annual crops against which introduced parasitoids have been established with unknown or partial success include the cotton aphid, *Aphis gossypii*, on taro (Wellings et al. 1994); *S. graminum*, and *R. maidis* on sorghum (Gilstrap et al. 1984, Zuniga 1990); the sow thistle aphid, *Hyperomyzus lactucae* L. in lettuce (Carver and Woolcock 1986); the cabbage aphid, *Brevicoryne brassicae* L. on cabbage (Clausen 1978); and *D. noxia* in cereal crops (e.g., Elliot et al. 1995, 1999, Pike et al. 1999, Brewer et al. 2001, Burd et al. 2001, Prinsloo et al. 2002), among others (Stary 1993).

In many classical biological control successes, the exotic pest does not reach damaging levels within its native range, because endemic natural enemies keep it under control. For example, Russian wheat aphid is not a pest in Europe, where it is apparently kept under control by a suite of natural enemies (Hopper et al. 1995, Kazmer et al. 1996, Chen and Hopper 1997, De Farias and Hopper 1997, 1999, Basky and Hopper 2000). Soybean aphid is a sporadic pest in China and southeast Asia and rarely if ever reaches pest status in Japan. There is some evidence that natural enemies can maintain soybean aphids at low densities in China (Liu et al. 2004, Wu et al. 2004) and Indonesia (van den Berg et al. 1997) in insecticide-free settings.

However, which, if any, natural enemies should be imported? Generalist natural enemies pose unacceptable risks to nontarget organisms (Follett and Duan 2000, Louda et al. 2003), but the level of specificity required to lower risk to an acceptable level given (1) the potential consequences of not achieving control and (2) the probability that the introduction will be successful in solving the pest problem has not been well-defined in arthropod biological control (van Driesche and Hoddle 2000, van Lenteren et al. 2003). In the case of aphid biological control, a number of insect natural enemies are known that are aphid specialists, i.e., species that feed only on members of the hemipteran superfamily Aphidoidea. The better-known groups include coccinellids (some members of the tribe Coccinellini), some cecidomyiid midges, species of syrphid flies in the subfamily Syrphinae, all members of the braconid subfamily Aphidiinae, and all members of the aphelinid genus *Aphelinus* (Hagen and van den Bosch 1968). Some other groups, such as chamaemyiids, anthocorids, chrysopids, and some coccinellids, feed on aphids as well as other small, soft-bodied insects. Among the aphid specialists, specificity for subgroups within the Aphidoidea is most consistently found in the aphidiine and *Aphelinus* parasitoids. In the next section, we review information on Eurasian aphidiine and *Aphelinus* parasitoids that are candidates for release against the soybean aphid.

The Parasitoids

Foreign exploration for soybean aphid natural enemies was conducted in Japan and China in 2001 and 2002. In Japan, R. J. O. and D. Voegtlin determined that

Table 2. Published host records for *L. gracilis* (Hymenoptera: Braconidae: Aphidiinae)

Subfamily	Tribe	Genus	Species
Aphidinae	Aphidini	<i>Aphis</i>	<i>affinis</i> Del Guercio, <i>bupleuri</i> Börner, <i>cisticola</i> Leclant and Remaudière, <i>confusa</i> Walker, <i>craccae</i> L., <i>craccivora</i> Koch, <i>euphorbiae</i> Kaltenbach, <i>fabae</i> Scopoli, <i>glycines</i> , <i>gossypii</i> , <i>hederae</i> Kaltenbach, <i>intybi</i> Koch, <i>newtoni</i> Theobald, <i>origani</i> Passerini, <i>plantaginis</i> Goeze, <i>polygonata</i> Nevsky, <i>pomi</i> De Geer, <i>ruborum</i> Börner, <i>salviae</i> Walker, <i>sedii</i> Kaltenbach, <i>solanella</i> Theobald, <i>spiraecola</i> Patch, <i>taraxacicola</i> Börner, sp.
		<i>Rhopalosiphum</i>	<i>padi</i> L.
		<i>Toxoptera</i>	<i>aurantii</i> (Boyer de Fonscolombe)
	Macrosiphini	<i>Acyrthosiphon</i>	<i>rubi</i> Narzikulov
		<i>Brachycaudus</i>	<i>amygdalinus</i> (Schouteden), <i>cardui</i> L., <i>helichrysi</i> (Kaltenbach), <i>mordwilkoii</i> HRL., <i>persicaecola</i> Biosduval, <i>prunicola</i> (Kaltenbach), sp.
		<i>Dysaphis</i>	<i>plantaginea</i> (Passerini)
		<i>Lipaphis</i>	<i>erysimi</i> (Kaltenbach)
		<i>Myzus</i>	<i>cerasi</i> (Fabricius), <i>persicae</i> (Sulzer)
		<i>Liosomaphis</i>	sp.
		<i>Machiatiella</i>	sp.
Anoeciinae	(none)	<i>Anoecia</i>	<i>corni</i> (F.), sp.
Eriosomatinae	Eriosomatini	<i>Eriosoma</i>	<i>Lanigerum</i> (Hausmann)
Calaphidinae	Panaphidini	<i>Therioaphis</i>	sp.

List compiled from the following sources: Stary 1966, 1967, 1979; Mackauer 1967; Mackauer and Stary 1967; Stary and Schlinger 1967; Takada and Rishi 1980; Stary and Ghosh 1983; Bhagat 1984; Chang et al. 1994. All recorded hosts are in the family Aphididae; classification as presented by Remaudière and Remaudière (1997) and Blackman and Eastop (2000).

predatory flies, an unidentified fungal agent, coccinellids, and at least two parasitoid species were common. In particular, one parasitoid species, *Aphelinus albipodus*, (Aphelinidae), was widely dispersed and reared from soybean aphids that were at very low densities in numerous fields. In China, G. E. H., D. W. R., and Z. W. also observed the presence of dipteran and coccinellid predators, as well as the parasitoids *Lysiphlebus fabarum* (Marshall) and *Lipolexis gracilis* Förster (Braconidae: Aphidiinae), both of which were active at extremely low soybean aphid densities. The parasitoids collected in both Japan and China were imported into quarantine in Newark, DE, and currently both *A. albipodus* and *L. gracilis* are in culture. In addition, non-Japanese strains of *A. albipodus* had been released against the Russian wheat aphid in the western United States in the early 1990s, and recoveries stemming from these releases were made in Wyoming in the summer of 2001. Individuals from this population successfully parasitized soybean aphid in the laboratory, and the USDA Animal and Plant Health Inspection Service (APHIS) began mass rearing this strain of *A. albipodus* on soybean aphid. By the 2002 field season, therefore, three parasitoid entities of Asian origin had passed through quarantine and were, in principle, available for release against soybean aphid in the field: two geographic strains of *A. albipodus* and one population of *L. gracilis*. In this section, we review the host range of these species.

Lipolexis gracilis is known from Europe to the Far East. It has a rather broad published host range within the aphidine tribes Aphidini and Macrosiphini and attacks some nonaphidine aphids as well (Table 2). As is common in host-parasitoid interactions, the host list compiled for Table 1 probably exceeds the host

range of any one geographic strain of *L. gracilis* because of host specialization within parasitoid strains (for examples of this phenomenon in other aphidiine braconids, see Carver 1984, Pungert 1984, Powell and Wright 1988). We are aware of only a single record of *L. gracilis* attacking soybean aphid, and this was in South Korea (Chang et al. 1994). Stary (1966) considered *L. gracilis* to be an especially valuable biological control agent of pest aphids because of its ability to colonize agricultural fields early in the growing season.

Aphelinus albipodus occurs throughout Asia and Eastern Europe, although it has been reported from Africa and South America as well (Hayat 1998). The host range of *A. albipodus* seems more restricted than that of *L. gracilis*, although it seems to be centered on the same aphid groups (Table 3). In recent work done as part of the Russian wheat aphid biological control project, four geographic strains of *A. albipodus* that had originally been collected from Russian wheat aphid were tested on 16 aphid species and adult parasitoids emerged from 9 to 14 species (depending on parasitoid strain) (Elliot et al. 1999). Two aphid species were consistently not attacked by *A. albipodus*: *Dactynotus* (*Uroleucon*) *helianthicola* Olive (Aphididae: Aphidinae: Microsiphini) and *Sipha flava* (Forbes) (Aphididae: Chaitophorinae) (Elliot et al. 1999). Our record of *A. albipodus* attacking soybean aphid seems to be a first record of this association. The Japanese strain of *A. albipodus* attacks and successfully develops within five pest aphids other than soybean aphid, and it either does not attack or cannot develop within the Russian wheat aphid (K. R. H., unpublished data). Recent data suggest, however, that *A. albipodus* and *A. varipes* (Förster) actually comprise a complex

Table 3. Published host records for *A. albipodus* (Hymenoptera: Aphelinidae)

Subfamily	Tribe	Genus	Species
Aphidinae	Aphidini	<i>Aphis</i>	<i>citricola</i> van der Goot, <i>fabae</i> , <i>glycines</i> , <i>gossypii</i> , <i>helianthi</i> Monell, <i>nerii</i> Boyer de Fonscolombe, <i>spiraeicola</i>
		<i>Rhopalosiphum</i>	<i>maidis</i> , <i>padi</i>
		<i>Schizaphis</i>	<i>graminum</i>
	Macrosiphini	<i>Acyrtosiphon</i>	<i>pisum</i>
		<i>Brevicoryne</i>	<i>brassicae</i>
		<i>Diuraphis</i>	<i>noxia</i> , <i>tritici</i> (Gillette)
		<i>Lipaphis</i>	<i>erysimi</i>
		<i>Myzus</i>	<i>persicae</i>
		<i>Sitobion</i>	<i>avenae</i> (Fabricius)
		<i>Therioaphis</i>	<i>trifolii</i> (Monell)
Callaphidinae	Panaphidini		

List compiled from the following sources: Hayat and Fatima 1992, Hayat 1998, Elliot et al. 1999, and our own observations. All recorded hosts are in the family Aphididae; classification as presented by Blackman and Eastop (2000).

of sibling species with different host ranges (Hopper et al. 1998, Zhu and Greenstone 1999, Chen et al. 2002). Despite this, we have found that the Japanese and ‘Wyoming’ strains of *A. albipodus* are reproductively compatible (Z. W. and G. E. H., unpublished data).

Summarizing the host range data, *L. gracilis* has a broader published host range than *A. albipodus*, but both species seem to be oligophagous, attacking a subset of aphidids in the subfamilies Aphidinae and Callaphidinae. For both species, geographic strains may show considerable restriction in host range with respect to a complete host list. Varying degrees of host specialization by geographic strains have been found in many insects (Fox and Morrow 1981), including a number of aphid parasitoids (Carver 1984, Pungertl 1984, Powell and Wright 1988, Kazmer et al. 1996), and such patterns have already been documented in the *A. albipodus* strains imported for Russian wheat aphid biological control (Elliot et al. 1999) and for a larger subset of members of the *A. albipodus/varipes* complex (K. R. H., unpublished data).

Of the three parasitoid entities in culture, one is already established in the United States. Populations of *A. albipodus* from Europe and central Asia were first introduced to the United States in 1990 to control Russian wheat aphid (Hopper et al. 1998, Prokrym et al. 1998) and became established in California, Colorado, Idaho, Kansas, Montana, Nebraska, Oklahoma, Oregon, Texas, Washington, and Wyoming (Prokrym et al. 1998, Burd et al. 2001). Individuals stemming from these releases were recovered in Wyoming in 2001 and were found to parasitize soybean aphid in the laboratory (Z. W. and G. E. H., unpublished data).

Releases of the ‘Wyoming’ strain of *A. albipodus* into soybean fields in Minnesota and Wisconsin were conducted in the summer of 2002. Our decision to redistribute this strain of *A. albipodus* was based on two lines of reasoning. First, we felt that the potential environmental costs of not achieving biological control of soybean aphid likely outweigh the environmental risks of moving this parasitoid from the western to the midwestern United States. Based on observations in Japan suggesting widespread attack of soybean

aphid at low host densities by *A. albipodus*, the status of this species as the dominant introduced natural enemy of Russian wheat aphid 10 yr after release, and encouraging laboratory results on soybean aphid, we felt that there was also a sufficiently high likelihood of achieving substantial biological control with *A. albipodus* to justify release. While the host range of this parasitoid is not particularly narrow, neither is it particularly broad compared with other aphid parasitoids. Also, the use of other pest aphids may actually improve the likelihood of establishment of *A. albipodus* in the midwestern United States. Second, we consider the likelihood to be relatively high that this ‘Wyoming’ strain of *A. albipodus* will spread from Russian wheat aphid to soybean aphid on its own for three reasons. First, the range of soybean aphid is expanding toward areas that harbor Russian wheat aphid. The eastern edge of the current Russian wheat aphid distribution extends into central South Dakota, Nebraska, Kansas, and Oklahoma. Meanwhile, the distribution of soybean aphid is expanding westward from an initial focal distribution centered around Michigan, Wisconsin, Minnesota, and into eastern North and South Dakota and western Iowa and Missouri (Venette and Ragsdale 2004). Third, like other strains of *A. albipodus*, the ‘Wyoming’ strain can use alternative hosts such as the corn leaf aphid that provide overlap with the distributions of both Russian wheat aphid and soybean aphid (see Table 3). Fourth, our experimental results have shown that the ‘Wyoming’ strain of *A. albipodus* reproduces well under conditions of high humidity in the laboratory (Z. W. and G. E. H., unpublished data). It is therefore unlikely that this strain will be prevented from expanding its distribution into midwestern or eastern regions based on an intolerance of increased humidity in these areas with respect to its current western distribution.

Conclusions

The attractiveness of importation biological control of soybean will increase with two factors: (1) the likelihood that biological control will be successful in regulating soybean aphid to low equilibrium densities and (2) the severity of the pest problem. Beyond the

potential attractiveness of biological control for aphid control and soybean production though, biological control agents have to be chosen so as to minimize the risk of unintended side effects. The best way to minimize these risks is to import a highly specific natural enemy. But what is the threshold of specificity required? And what if high specificity compromises effectiveness by (for instance), limiting opportunities for the natural enemy to use alternative aphid species for overwintering purposes? Specificity thresholds are quite stringent for weed biological control (McFayden 1998) but have not yet been widely discussed in the context of arthropod biological control (but see van Driesche and Hoddle 1997, Sands and van Driesche 2000). In our view, specificity thresholds will have to be established within a risk analysis framework, where the best possible solution is sought given multiple constraints. Constraints faced by managers of invasive species and biological control practitioners include the fact that an invasion (by the pest) has already occurred, the fact that the absence of action is not necessarily neutral, and the fact that natural enemies available for importation are biological entities that may have limitations with respect to immediate goals. To these constraints must be added practical considerations related to the logistics and economics of doing the research that may be needed to formulate a realistic risk analysis.

We are not yet ready to define a specificity threshold for soybean aphid natural enemies, but it is clear that the threshold will not be a single number, but rather the outcome of a function (either formal or informal) that incorporates the likelihood of success and the balance between environmental risks incurred and averted. Other technical issues concerning specificity thresholds that will have to be worked out include the phylogenetic relatedness between species that are attacked. Clearly, a host list that includes 20 species that are all in the same genus is qualitatively different from a host list of 20 species scattered over multiple genera. It would also be naive to say that all nontarget species share equal weight as risk factors. Nontarget species that are endangered or threatened, species known to play important roles in ecosystem function, or species of special esthetic, educational, or cultural value may raise red flags before a quantitative specificity threshold is reached.

Our ability to formulate a clear concept of the specificity needed to justify biological control in our system will increase as soybean aphid settles into a more predictable pattern as a pest in North America and as we continue to study its natural enemies. Specific research goals beyond host and prey range testing of imported natural enemies under quarantine include determination of factors that regulate soybean aphids in their native Asia and assessment of the role of endemic natural enemies in North America, which include native generalist predators and parasitoids and two Asian species: the non-native coccinellid *Harmonia axyridis* and the 'Wyoming' strain of *A. albipodus*.

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